





## Article

# Spatial Ecology of the Association between Demosponges and *Nemalécium lighti* at Bonaire, Dutch Caribbean

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**Abstract:** Coral reefs are known to be among the most biodiverse marine ecosystems and one of the richest in terms of associations and species interactions, especially those involving invertebrates such as corals and sponges. Despite that, our knowledge about cryptic fauna and their ecological role remains remarkably scarce. This study aimed to address this gap by defining for the first time the spatial ecology of the association between the epibiont hydrozoan *Nemalécium lighti* and the Porifera community of shallow coral reef systems at Bonaire. In particular, the host range, prevalence, and distribution of the association were examined in relation to different sites, depths, and dimensions of the sponge hosts. We report *Nemalécium lighti* to be in association with 9 out of 16 genera of sponges encountered and 15 out of 16 of the dive sites examined. The prevalence of the hydroid–sponge association in Bonaire reef was 6.55%, with a maximum value of over 30%. This hydrozoan has been found to be a generalist symbiont, displaying a strong preference for sponges of the genus *Aplysina*, with no significant preference in relation to depth. On the contrary, the size of the host appeared to influence the prevalence of association, with large tubular sponges found to be the preferred host. Although further studies are needed to better understand the biological and ecological reason for these results, this study improved our knowledge of Bonaire’s coral reef cryptofauna diversity and its interspecific associations.

**Keywords:** coral reef; cryptofauna; sponges; hydrozoa; *Aplysina*; prevalence; symbiosis



**Citation:** Gobbato, J.; Magrini, A.; García-Hernández, J.E.; Viridis, F.; Galli, P.; Seveso, D.; Montano, S. Spatial Ecology of the Association between Demosponges and *Nemalécium lighti* at Bonaire, Dutch Caribbean. *Diversity* **2022**, *14*, 607. <https://doi.org/10.3390/d14080607>

Academic Editors: Harilaos Lessios and Michael Wink

Received: 25 June 2022

Accepted: 26 July 2022

Published: 28 July 2022

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## 1. Introduction

Coral reefs are recognized as one of the most important marine ecosystems on the planet, since they host the highest biodiversity among marine environments [1]. The complex topography created by the living organisms, such as cnidarians and sponges, provides a three-dimensional structure that supports an incredible diversity of organisms, well suited for species interactions and associations [2]. Unfortunately, this fundamental environment is experiencing severe degradation due to the impacts directly related to climate change and anthropogenic activities [3]. As these ecosystems disappear, scientists find themselves racing against time to increase our knowledge of cryptofauna ecological interactions and their potential role in the survival and resilience of the reef ecosystem [4]. For example, hermatypic corals have evolved crucial microbial symbiotic relationships in order to maintain their health status, improve energy production, cope with environmental changes, complete nutrient recycling, have a defense mechanism for predators, or as a

protection from potential pathogen agents and coral feeding organisms [5–8]. Additionally, stony corals have also developed a symbiotic association with several distinct phyla that are involved such as Cnidaria, Porifera, Echinodermata, Annelida, Arthropoda, and Mollusca [9].

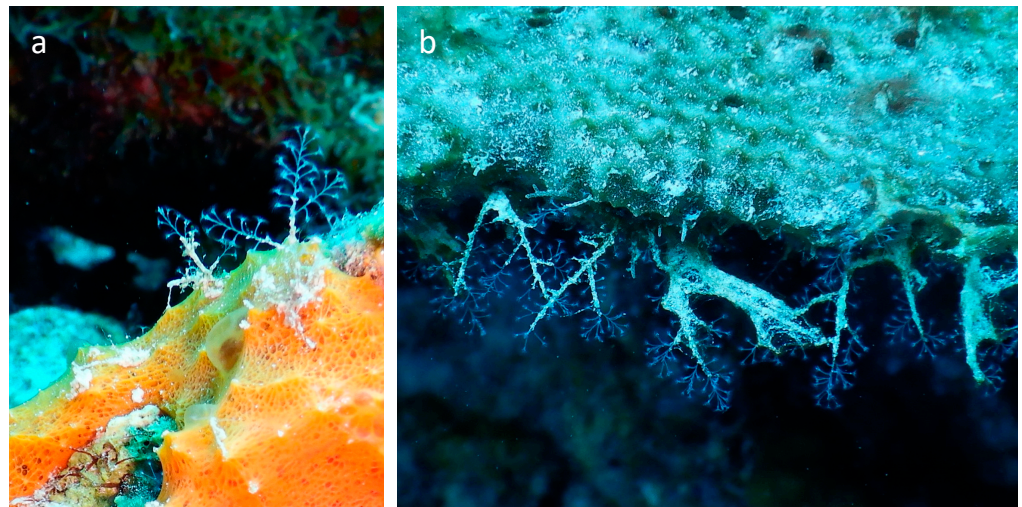
Hydrozoans are an example of a group of organisms that has been able to develop a plethora of symbiotic relationships with several marine organisms [10,11], including scleractinians and sponges [12–14]. Currently, there are records for a total of 20 hydrozoan families and 50 genera involved in symbiotic associations with different animals worldwide [15]. Sponges emerged as a suitable host due to the constant water filtration, which results in the continuous presence of nutrients that are available to its symbionts [15,16]. In particular, there are six families of hydrozoans that are generally found in relation to sponges (Cytaeidae, Corynidae, Cladonematidae, Tubulariidae, Sphaerocorynidae, and Campanulariidae) [16]. Worldwide, a total of 26 species of hydrozoans have been identified as epibionts of sponges; however, little information is known about most of these associations [16,17].

Bonaire coral reef systems have recently been recognized as one of the most biodiverse, robust, resilient, and healthy ecosystems in the South Caribbean region [18]. In this context, the island serves as an interesting hotspot to study hydrozoan–sponge associations, since sponges are one of the dominant benthic groups on the reef, second only to corals [19]. Recently, several studies have been conducted identifying novel symbiotic relationships between the reef organisms, such as the zoantharian *Parazoanthus axinellae* epibiotic on the sponge of the genus *Axinella* [16], *Pteroclava krempfi* with alcyonaceans [20], the sponge *Agelas conifera* and the agariciid corals *Agaricia agaricites* and *Helioseris cucullata* [21], the coral-gall crab *Opecarcinus hypostegus* and the agariciid *Agaricia undata* [22], crabs of the genus *Platypodiella* and zoantharians of the genus *Palythoa* with the sponge *Niphates digitalis* [23], sponges, scleractinians, ascidians and zoantharians with polychaetes *Spirobranchus* [24,25], and the *Stylaster–Millepora* association first reported in Bonaire [26]. Nevertheless, coral reef-associated fauna remain strongly understudied, and the total number of species of micro- and macro-invertebrates involved in association with other reef organisms in this region remains largely unknown, despite the potential benefit that these cryptic associations may have on the survival and resilience of the coral reef ecosystems [4,8]. One of these understudied organisms is *Nemalecium lighti* (Hargitt, 1924), a common thecate hydroid species belonging to the Haleciidae family that can be found all year round in all tropical waters, constituting one of the most abundant hydroid species [27,28]. *N. lighti* can be usually found on reef rock substrate, on corals, and on sponge surfaces, where it can better exploit the presence of planktonic particles to feed in the water column [29,30]. Its presence seems to have no influence on the functionality of the feeding strategy of the sponge host, as already demonstrated for other hydrozoans species [16,30], but see [31]. Therefore the impact of these associations on the sponges appears negligible, or even beneficial in some cases, as it may act as protection from predators thanks to the hydrozoan nematocysts [30,32].

In light of this, there are few studies that have examined the spatial ecology of cryptic invertebrates associated with sponges [33,34]. Therefore, the goal of this study was to investigate and characterize the association of *Nemalecium lighti* with sponges in the coral reefs of Bonaire Island, with particular attention focused on determining the host range, prevalence, and distribution of this association. The results obtained provide a foundation for additional studies aimed at bridging the gap in our understanding concerning the cryptofauna diversity and its fundamental ecological role in coral reef ecosystems.

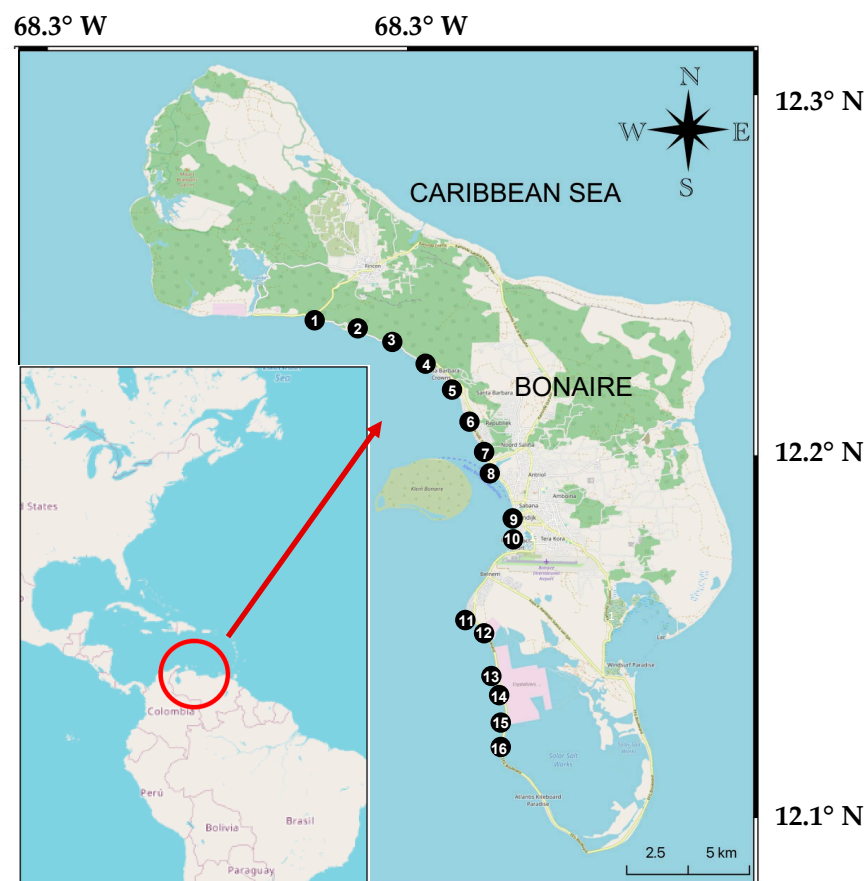
## 2. Materials and Methods

Underwater surveys were conducted between May and August 2021 to investigate the prevalence and distribution of *Nemalecium lighti*–sponge associations (Figure 1) in the reef system around Bonaire Island (12°12' N, 68°35' W), an area which is entirely protected since 1979 as part of the Bonaire National Marine Park (BNMP) [18].



**Figure 1.** Two examples of the association between demosponges and *Nemalecium lighti* in Bonaire reef system: *N. lighti* associated with (a) *Scopalina ruetzleri* and (b) *Ircinia* sp.

Along the west coast of the island, 16 different sites were chosen randomly based on their SCUBA shore-diving accessibility (Figure 2 and Table 1).



**Figure 2.** Map of Bonaire, Dutch Caribbean (12°12' N, 68°35' W) highlighting the dive sites investigated for sponges–*Nemalecium lighti* association in this study. Map made from OpenStreetMap loaded into QGIS.

**Table 1.** Coordinates, maximum and mean value of prevalence of association between sponges and *Nemalécium lighti* for each of the dive sites considered for the analyses in the study area.

N°	Dive Sites	Coordinates	Maximum Prevalence (%)	Mean Prevalence (% ± SE)
1	Tolo Reef (Tol)	12°12'92" N; 068°20'22" W	15.38	4.89 ± 2.68
2	Jeff Davies Memorial (JDM)	12°12'18" N; 068°18'50" W	8.33	2.67 ± 1.69
3	Oil Slick Leap (OSL)	12°12'03" N; 068°18'51" W	5.55	0.93 ± 0.93
4	Andrea I (AI)	12°11'29" N; 068°17'80" W	12.50	2.08 ± 2.08
5	Andrea II (AII)	12°11'18" N; 068°17'48" W	13.33	2.22 ± 2.22
6	La Machaca (LM)	12°10'20" N; 068°17'22" W	17.86	8.67 ± 2.73
7	Buddy's Reef (BM)	12°10'14" N; 068°17'18" W	16.67	4.01 ± 2.81
8	Bari Reef (BF)	12°10'04" N; 068°17'10" W	33.33	20.82 ± 3.56
9	Something Special (SS)	12°09'70" N; 068°17'02" W	3.70	2.12 ± 0.70
10	Town Pier (TP)	12°08'57" N; 068°16'40" W	2.63	0.44 ± 0.44
11	Punt Viekant (PV)	12°06'91" N; 068°17'66" W	0.00	0.00 ± 0.00
12	Alice in Wonderland (AiW)	12°05'99" N; 068°17'12" W	22.22	17.59 ± 2.31
13	Salt Pier (SP)	12°05'01" N; 068°16'91" W	9.52	4.37 ± 2.01
14	Invisibles (I)	12°04'65" N; 068°16'80" W	17.65	2.94 ± 2.94
15	Tori Reef (Tor)	12°04'25" N; 068°16'84" W	10.00	1.67 ± 1.67
16	Pink Beach (PB)	12°03'85" N; 068°16'90" W	11.11	5.56 ± 1.87

Quantitative analyses were conducted by SCUBA diving, randomly placing three belt transects of 25 m × 2 m at two different depths for each site (total = 96 transects), resulting in 16 “shallow” stations between a 5–9 m depth and 16 “deep” stations between a 10–15 m depth.

Every sponge individual encountered within our transects, including without the presence of *Nemalécium lighti*, was counted. The prevalence was calculated as the number of sponges associated with *N. lighti* divided by the total number of sponges counted at that specific time and place. In addition, the taxon-specific prevalence for each sponge's genus was calculated as the number of sponge hosting associations for each genus, divided by the total number of counted sponges belonging to the same genus, according to Montano et al. 2016 [20]. All sponges were photographed in situ and were identified at the genus level using the relevant literature [35]. Sponges were included in the dataset and counted only when 50% of the individual or more lay within the belt transect area. Furthermore, the potential relationship between the association and the host size was evaluated through a comparison of the observed prevalence with that of five sponge size classes (C1: 5–10 cm; C2: 10–20 cm; C3: 20–30 cm; C4: 40–50 cm; C5: > 50 cm). The size of the sponges was estimated by placing a tape measure on the side of each specimen.

All the data obtained were tested for normality with Kolmogorov–Smirnov tests. In case the normal distribution and homogeneity of variance was violated, Kruskal–Wallis and Mann–Whitney *U* tests were performed to analyze the mean differences between the sites, depths, and dimensions of the sponge host. Data are presented as the arithmetic mean ± standard error unless stated otherwise. All the statistical analysis performed for this study were conducted using IBM SPSS 27 Software (IBM SPSS 27, New York, NY, USA).

### 3. Results

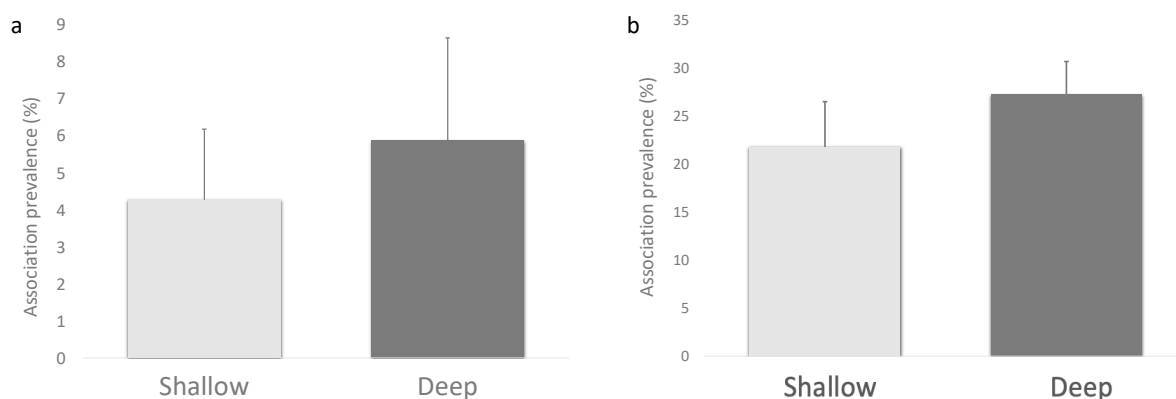
In the area investigated, a total of 1755 sponges belonging to the class of Demospongiae were counted and classified in 14 families belonging to 16 different genera, with *Scopalina* (26.67%), *Aplysina* (14.30%), *Agelas* (13.16%), and *Aiolochoira* (9.46%) emerging as the more abundant, while the remaining genera only represented under 7% of the sponges found in the area (Table 2).

**Table 2.** Genera of sponges considered for the analyses in the study area with values of relative abundance, maximum and mean prevalence of association with *Nemalécium lighti*.

Genus	Relative Abundance (%)	Maximum Prevalence (%)	Mean Prevalence (% ± SE)
<i>Agelas</i>	13.16	7.27	2.70 ± 1.12
<i>Aiolochoiria</i>	9.46	8.62	4.09 ± 1.69
<i>Aplysina</i>	14.30	36.17	26.06 ± 4.76
<i>Callyspongia</i>	3.13	0.00	0.00 ± 0.00
<i>Clathria</i>	0.23	0.00	0.00 ± 0.00
<i>Cliona</i>	0.40	25.00	5.00 ± 4.56
<i>Desmapsamma</i>	4.05	8.69	2.74 ± 1.62
<i>Ectyoplasia</i>	3.82	0.00	0.00 ± 0.00
<i>Halisarca</i>	0.17	0.00	0.00 ± 0.00
<i>Iotrochota</i>	4.73	4.00	0.80 ± 0.73
<i>Ircinia</i>	6.38	5.88	2.81 ± 1.01
<i>Monanchora</i>	0.46	0.00	0.00 ± 0.00
<i>Niphates</i>	6.84	0.00	0.00 ± 0.00
<i>Phorbas</i>	0.11	0.00	0.00 ± 0.00
<i>Scopalina</i>	26.67	4.11	1.78 ± 0.76
<i>Verongula</i>	6.09	15.38	6.98 ± 2.34

The genus *Scopalina* resulted as being the most abundant and prevalent group in both the shallow and the deep, with values of, respectively, 27.82% and 26.51% (Table 2). The genus *Agelas* showed a completely different distribution in relation to depth with a relative abundance of 5.45% in the shallow stations and 19.34% in the deep ones (Table 2). A similar trend was observed for *Niphates*, with an increase of the relative abundance from 4.66% in the shallow stations to 8.92% in the deep stations. The genera *Clathria*, *Cliona*, *Halisarca*, *Monanchora*, and *Phorbas* were extremely poorly represented in the study area at both depths, with *Halisarca* resulting as being the only genus completely absent in the shallow stations. Moreover, the spatial distribution of sponges between deep and shallow stations showed different trends for *Agelas*, *Desmapsamma*, *Ectyoplasia*, and *Niphates* at the two depths considered for the study, even if they were not statistically significant (Kruskal–Wallis test,  $p > 0.05$ ).

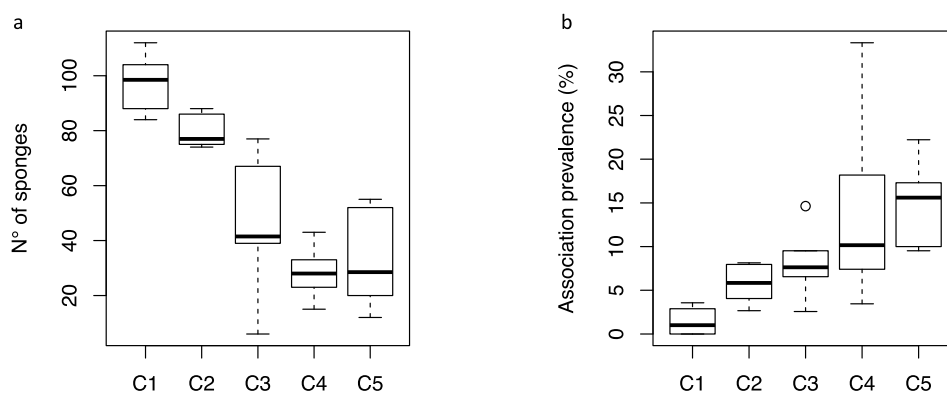
Regarding the sponge–hydroid interactions, *Nemalécium lighti* has been found in association with 9 out of 16 genera of sponges and in 15 out of 16 of the dive sites surveyed. A total of 115 sponge individuals hosted at least one colony of *N. lighti*. The prevalence of the occurrence of the hydroid–sponge association in the Bonaire reef was 6.55%, with a maximum value of 33.33%. The mean prevalence of the association on the analyzed reef sites was  $5.06 \pm 1.91\%$ . Among them, “Bari Reef” (BR), “Alice in Wonderland” (AiW), and “La Machaca” (LM) showed higher values with, respectively,  $20.82 \pm 3.56\%$ ,  $17.59 \pm 2.31\%$ , and  $8.67 \pm 2.72\%$ , with the others showing less than 6% (Table 1). However, the differences of prevalence among the tested sites were not statistically significant (Kruskal–Wallis test,  $p > 0.05$ ). With regards to the depths considered, the mean prevalence for the deep stations resulted in being higher compared to the shallow stations with, respectively,  $5.86 \pm 2.77\%$  and  $4.27 \pm 1.91\%$  (Figure 3a), even if the differences between the stations were not statistically significant both in relation to the site and genera (Mann–Whitney Test,  $p > 0.05$ ).



**Figure 3.** Prevalence of *Nemalecium lighti*–sponges association in the study area: (a) Mean association prevalence for all the genera considered and (b) for the genus *Aplysina* in relation to depth.

Furthermore, the taxon-specific prevalence was calculated for each genus of sponge that was found to be the host of the association (Table 2). Sponges belonging to the genus *Aplysina* were the most involved in the association with *N. lighti*, with a prevalence of  $21.76 \pm 4.72\%$  in shallow stations and  $27.22 \pm 3.44\%$  in the deep stations (Figure 3b). Similarly, *Verongula* and *Aiolochoxia* were the second most involved in association with *N. lighti*, even if not notably in the shallow stations. By contrast, *Cliona* showed an elevated prevalence in the shallow station and no association in the deep station. There were seven genera (*Callyspongia*, *Clathria*, *Ectyoplasia*, *Halisarca*, *Monanchora*, *Niphates*, and *Phorbas*) that did not show an association in either the shallow stations or the deep stations, whereas the *Iotrochota*–*Nemalecium lighti* association was found only in deep stations. The differences in the prevalences among the analyzed genera were tested as being statistically significant (Kruskal–Wallis Test,  $p < 0.05$ ).

When correlating the sponge dimension with the *N. lighti* association, most of the sponges belonged to the smaller size classes of 5–30 cm (~70%), whereas only a minor part of the sponges was comprised in the larger size classes of 40–50 cm (Figure 4a). Despite this, a positive increase in prevalence was recorded, with values of  $1.41 \pm 0.66\%$ ,  $5.75 \pm 0.79\%$ ,  $8.09 \pm 1.62\%$ ,  $13.78 \pm 4.40\%$ , and  $15.04 \pm 1.96\%$  for C1 to C5 size classes, respectively (Figure 4b). Furthermore, the sponges belonging to the genus *Aplysina* showed a particular behavior in this regard, being the only genus with association cases in all the size classes, in both shallow and deep stations.



**Figure 4.** Hosts' size class distribution and prevalence analyses in the study area: (a) Number of sponges for each class size; (b) Prevalence of *Nemalecium lighti*–sponges association in relation to the host class size. The bold line in the middle of the boxes is the median value, the bottom part of the boxes is the lower quartile, the top part of the boxes is the upper quartile, the lines departing from the boxes are the lower and upper extremes, and the circle is an outlier value.

#### 4. Discussion

Over the years, multiple studies have addressed the role of coral reef biodiversity and its overall impact on the health of these ecosystems [1,4,9]. More specifically, Bonaire coral reef ecosystems emerged as an incredible source of rare or previously unreported reef organism associations. In this perspective, this study assessed for the first time the distribution, host range, and prevalence of the sponges–*Nemalecium lighti* association in this region, aiming to partially fill the knowledge deficiency about cryptofauna associations involving sponges and hydrozoans. The surveys revealed associations between host sponges and *N. lighti* at all the explored sites except one, suggesting a widespread distribution for the association all along the west coast of Bonaire, with some sites showing notably high values of prevalence (BR, AiW, and LM). The host range of this association accounts for nine genera belonging to the class Demospongiae, suggesting that *N. lighti* can be considered as a generalist, since it appears to not target a specific sponge species, at least within the depth ranges we conducted our surveys in. The spatial distribution of the hydroids along the reef zonation has been addressed in previous studies, revealing that different environmental conditions and depths may have an impact on the development of associations and the peculiar assemblage of hydroid species [36–38]. In particular, it has been observed that the maximum diversity of hydrozoans and related associations with sponges was reached on the reef slope, with a continued increase with the depth until reaching 30 m [29]. Similarly, in the present study, the prevalence of associations is slightly higher in the deep stations compared to the shallow ones. However, this result needs to be confirmed in future studies by considering not only the shallower part of the coral reefs but extending the surveys to mesophotic depths. In addition, considering that *N. lighti* is a small cryptic hydroid species growing to a maximum 2 cm that settles on the surface of sponges but sometimes also in protected and shaded parts of their structure, it cannot be excluded that some of the interactions may have been overlooked during our surveys, resulting in an underestimation of its actual prevalence.

The taxon-specific prevalence revealed that the highest prevalence of occurrence of the *N. lighti*–sponge association was observed with the genus *Aplysina* (26%). This prevalence value was almost four times higher than for the second genus involved in the association (*Verongula* with  $6.98 \pm 2.34\%$ ) and extremely more significant than for all the other species, which showed prevalence values lower than 5%. Sponges of the genus *Aplysina* represent an abundant and important component of the marine coastal ecosystems in tropical and subtropical waters [39], where they contribute to the three-dimensionality of the reef structure, which is fundamental for hosting and sustaining several species of associated fauna. The preference of *N. lighti* for this genus may be the result of the complex tubular growth morphology that exposes the epibiont hydroid to a strong current and water flow, characteristics usually exploited by this species [16,40].

In addition, sponges are known to produce an array of chemicals and metabolic products that are ecologically important for different purposes (e.g., growth, protection, competition) [41]. Among them, sponges belonging to the genus *Aplysina* are known to produce high concentrations of brominated alkaloids metabolites (up to 13% of the dry weight) related to antimicrobial activity and cytotoxic activity [42]. These sponges probably produce them as a chemical defense, biofouling, and deterrent against fish predators, as tested on *Thalassoma bifasciatum* and *Blennius sphinx* [43–49]. This peculiar characteristic of the *Aplysina* sponges may be one of the factors that enhances the association with *N. lighti*, as it may take advantage of this defense mechanism of the host to protect itself from predators or microbial offense [50]. However, future investigations to test this hypothesis and to elucidate the nature of this association in the reefs of Bonaire are needed.

Finally, the observed increase in prevalence related to the dimension of the sponges suggests that other factors pertaining to the host also determine the ability of *N. lighti* to settle on sponges. In particular, an increase in sponge (species-dependent) size may correspond to an increase of the favorable surface on which the hydroids can establish the association. In addition, the amount of time necessary for the sponge to grow may also be

a contributing factor for the settlement of larvae, increasing the probability of growth on the sponge surface. Further studies are needed to test both of the scenarios proposed and to clearly understand the effect of host size on this particular association.

## 5. Conclusions

This study provides the first characterization and quantification of the association between the cryptic hydrozoan *Nemalecium lighti* and the demosponge community within the coral reef systems of Bonaire. This hydrozoan has been found to be a generalist symbiont of different genera of sponge along the west coast of Bonaire. Even though the differences in the prevalence of occurrence of the associations were not significantly important with regards to the depth, future investigations extending into the deeper parts of the reef, including mesophotic depths, may be important to better define the role of depth in this association. However, the dimension of the host resulted in influencing the prevalence of association, with a large tubular sponge found to be the preferred host for *N. lighti*. Moreover, the taxon-specific prevalence revealed that the genus most involved in the association with *N. lighti* was *Aplysina*, with an extremely higher prevalence value compared to the other genera recorded. This may be associated with the production of brominated alkaloid metabolites that serve as antimicrobial and biofouling as well as chemical protection from predators. Additional studies are needed to better understand the implications of this preference and what the main biological and ecological reasons for these results are. Overall, this study improves our understanding of the cryptofauna diversity of coral reef associations in Bonaire.

**Author Contributions:** Conceptualization, J.G. and S.M.; validation, J.E.G.-H., S.M. and D.S.; formal analysis, J.G. and A.M.; investigation, A.M. and F.V.; writing—original draft preparation, J.G.; writing—review and editing, S.M., J.E.G.-H. and D.S.; supervision, S.M., F.V. and P.G. All authors have read and agreed to the published version of the manuscript.

**Funding:** This research received no external funding.

**Data Availability Statement:** Not applicable.

**Acknowledgments:** The authors would like to thank Reef Renewal Bonaire Foundation for the logistic support provided. AM is grateful to Giorgia Ferrari and Camilla Rinaldi for the unique help during the field activities.

**Conflicts of Interest:** The authors declare no conflict of interest.

## References

1. Fisher, R.; O'Leary, R.A.; Low-Choy, S.; Mengersen, K.; Knowlton, N.; Brainard, R.E.; Caley, M.J. Species richness on coral reefs and the pursuit of convergent global estimates. *Curr. Biol.* **2015**, *25*, 500–505. [[CrossRef](#)]
2. Stella, J.S.; Jones, G.P.; Pratchett, M.S. Variation in the structure of epifaunal invertebrate assemblages among coral hosts. *Coral Reefs* **2010**, *29*, 957–973. [[CrossRef](#)]
3. Caley, M.J.; Buckley, K.A.; Jones, G.P. Separating ecological effects of habitat fragmentation, degradation, and loss on coral commensals. *Ecology* **2001**, *82*, 3435–3448. [[CrossRef](#)]
4. Montano, S. The Extraordinary Importance of Coral-Associated Fauna. *Diversity* **2020**, *12*, 357. [[CrossRef](#)]
5. Spotte, S. Supply of regenerated nitrogen to sea anemones by their symbiotic shrimp. *J. Exp. Mar. Biol. Ecol.* **1996**, *198*, 27–36. [[CrossRef](#)]
6. Rouzé, H.; Lecellier, G.; Mills, S.C.; Planes, S.; Berteaux-Lecellier, V.; Stewart, H. Juvenile *Trapezia* spp. crabs can increase juvenile host coral survival by protection from predation. *Mar. Ecol. Prog. Ser.* **2014**, *515*, 151–159. [[CrossRef](#)]
7. Pollock, F.J.; Katz, S.M.; Bourne, D.G.; Willis, B.L. *Cymo melanodactylus* crabs slow progression of white syndrome lesions on corals. *Coral Reefs* **2013**, *32*, 43–48. [[CrossRef](#)]
8. Montano, S.; Fattorini, S.; Parravicini, V.; Berumen, M.L.; Galli, P.; Maggioni, D.; Arrigoni, R.; Seveso, D.; Strona, G. Corals hosting symbiotic hydrozoans are less susceptible to predation and disease. *Proc. R. Soc. Biol. Sci.* **2017**, *284*, 20172405. [[CrossRef](#)]
9. Stella, J.S.; Pratchett, M.S.; Hutchings, P.A.; Jones, G.P. Coral-associated invertebrates: Diversity, ecological importance, and vulnerability to disturbance. *Oceanogr. Mar. Biol. Annu. Rev.* **2011**, *49*, 43–104.
10. Bo, M.; Di Camillo, C.G.; Puce, S.; Canese, S.; Giusti, M.; Angiolillo, M.; Bavestrello, G. A tubulariid hydroid associated with anthozoan corals in the Mediterranean Sea. *Ital. J. Zool.* **2011**, *78*, 487–496. [[CrossRef](#)]



11. Reimer, J.D.; Wee, H.B.; García-Hernández, J.E.; Hoeksema, B.W. Zoantharia (Anthozoa: Hexacorallia) abundance and associations with Porifera and Hydrozoa across a depth gradient on the west coast of Curaçao. *Syst. Biodivers.* **2018**, *16*, 820–830. [[CrossRef](#)]
12. Montano, S.; Arrigoni, R.; Pica, D.; Maggioni, D.; Puce, S. New insights into the symbiosis between *Zanclaea* (cnidaria, hydrozoa) and scleractinians. *Zool. Scr.* **2015**, *44*, 92–105. [[CrossRef](#)]
13. Montano, S.; Seveso, D.; Galli, P.; Puce, S.; Hoeksema, B.W. Mushroom corals as newly recorded hosts of the hydrozoan symbiont *Zanclaea* sp. *Mar. Biol. Res.* **2015**, *11*, 773–779. [[CrossRef](#)]
14. Montano, S.; Maggioni, D.; Arrigoni, R.; Seveso, D.; Puce, S.; Galli, P. The hidden diversity of *Zanclaea* associated with scleractinians revealed by molecular data. *PLoS ONE* **2015**, *10*, e0133084. [[CrossRef](#)] [[PubMed](#)]
15. Puce, S.; Cerrano, C.; Di Camillo, C.G.; Bavestrello, G. Hydroidomedusae (Cnidaria: Hydrozoa) symbiotic radiation. *J. Mar. Biol. Assoc. UK* **2008**, *88*, 1715–1721. [[CrossRef](#)]
16. Puce, S.; Calcinai, B.; Bavestrello, G.; Cerrano, C.; Gravili, C.; Boero, F. Hydrozoa (Cnidaria) symbiotic with Porifera: A review. *Mar. Ecol.* **2005**, *26*, 73–81. [[CrossRef](#)]
17. Villamizar, E.; Laughlin, R.A. Fauna Associated with the Sponges *Aplysina archeri* and *Aplysina lacunosa* in a Coral Reef of the Archipelago de Los Roques, National Park, Venezuela. In *Fossil and Recent Sponges*, 1st ed.; Reitner, J., Keupp, H., Eds.; Springer: Berlin/Heidelberg, Germany, 1991; pp. 522–542. [[CrossRef](#)]
18. IUCN. Coral Reef Resilience Assessment of the Bonaire National Marine Park. *Netherlands Antilles*. 2011. Available online: <https://data.iucn.org/dbtw-wpd/edocs/2011-008.pdf> (accessed on 23 May 2022).
19. Frade, P.R.; Bongaerts, P.; Baldwin, C.C.; Trembanis, A.C.; Bak, R.P.M.; Vermeij, M.J.A. Bonaire and Curaçao. In *Mesophotic Coral Ecosystems*, 1st ed.; Loya, Y., Puglise, K., Bridge, T., Eds.; Series Coral Reef of the World; Springer: Cham, Switzerland, 2019; pp. 149–162. [[CrossRef](#)]
20. Montano, S.; Allevi, V.; Seveso, D.; Maggioni, D.; Galli, P. Habitat preferences of the *Pteroclava kremppi*-alcyonaceans symbiosis: Inner vs outer coral reefs. *Symbiosis* **2017**, *72*, 225–231. [[CrossRef](#)]
21. García-Hernández, J.E.; van Moorsel, G.W.N.M.; Hoeksema, B.W. Lettuce corals overgrowing tube sponges at St. Eustatius, Dutch Caribbean. *Mar. Biodivers.* **2017**, *47*, 55–56. [[CrossRef](#)]
22. García-Hernández, J.E.; de Gier, W.; van Moorsel, G.W.N.M.; Hoeksema, B.W. The scleractinian *Agaricia undata* as a new host for the coral-gall crab *Opeparcinus hypostegus* at Bonaire, southern Caribbean. *Symbiosis* **2020**, *81*, 303–311. [[CrossRef](#)]
23. Garcia-Hernandez, J.E.; Reimer, J.D.; Hoeksema, B.W. Sponges hosting the zoantharia-associated crab *Platypodiella spectabilis* at St. Eustatius, Dutch Caribbean. *Coral Reefs* **2016**, *35*, 209–210. [[CrossRef](#)]
24. García-Hernández, J.E.; Hoeksema, B.W. Sponges as secondary hosts for Christmas tree worms at Curaçao. *Coral Reefs* **2017**, *36*, 1243–1244. [[CrossRef](#)]
25. Hoeksema, B.W.; García-Hernández, J.E.; van Moorsel, G.W.N.M.; Olthof, G.; ten Hove, H.A. Extension of the recorded host range of Caribbean Christmas tree worms (*Spirobranchus* spp.) with two scleractinians, a zoantharian, and an ascidian. *Diversity* **2020**, *12*, 115. [[CrossRef](#)]
26. Montano, S.; Reimer, J.D.; Ivanenko, V.N.; García-Hernández, J.E.; van Moorsel, G.W.N.M.; Galli, P.; Hoeksema, B.W. Widespread occurrence of a rarely known association between the hydrocorals *Stylaster roseus* and *Millepora alcornonis* at Bonaire, Southern Caribbean. *Diversity* **2020**, *12*, 218. [[CrossRef](#)]
27. Gravier-Bonnet, N.; Bourmaud, C.A.F. Hydroids (Cnidaria, Hydrozoa) of Coral Reefs: Preliminary Results on Community Structure, Species Distribution and Reproductive Biology in Juan de Nova Island (Southwest Indian Ocean). *West. Indian Ocean J. Mar. Sci.* **2006**, *5*, 123–132. [[CrossRef](#)]
28. Coma, R.; Ribes, M.; Orejas, C.; Gili, J.M. Prey capture by a benthic coral reef hydrozoan. *Coral Reefs* **1999**, *18*, 141–145. [[CrossRef](#)]
29. Di Camillo, C.G.; Bavestrello, G.; Valisano, L.; Puce, S. Spatial and temporal distribution in a tropical hydroid assemblage. *J. Mar. Biol. Assoc. UK* **2008**, *88*, 1589–1599. [[CrossRef](#)]
30. Bouillon, J.; Gravili, C.; Pagès, F.; Gili, J.M.; Boero, F. *An Introduction to Hydrozoa*, 1st ed.; Betsch, J.M., Bouchet, P., Énard, C., Eds.; Mémoires du Muséum national d'histoire naturelle: Paris, France, 2006.
31. Lewis, T.B.; Finelli, C.M. Epizotic zoanthids reduce pumping in two Caribbean vase sponges. *Coral Reefs* **2015**, *34*, 291–300. [[CrossRef](#)]
32. Puyana, M.; Fenical, W.; Pawlik, J.R. Are there activated chemical defenses in sponges of the genus *Aplysina* from the Caribbean? *Mar. Ecol. Prog. Ser.* **2003**, *246*, 127–135. [[CrossRef](#)]
33. Wulff, J.L. Ecological interactions of marine sponges. *Can. J. Zool.* **2006**, *84*, 146–166. [[CrossRef](#)]
34. Padua, A.; Lanna, E.; Klautau, M. Macrofauna inhabiting the sponge *Paraleucilla magna* (Porifera: Calcarea) in Rio de Janeiro, Brazil. *J. Mar. Biol. Assoc. UK* **2013**, *93*, 889–898. [[CrossRef](#)]
35. Zea, S.; Henkel, T.P.; Pawlik, J.R. The Sponge Guide: A Picture Guide to Caribbean Sponges. Available online: <https://www.spongeguide.org> (accessed on 21 January 2022).
36. Calder, D.R. Local distribution and biogeography of the hydroids (Cnidaria) of Bermuda. *Caribb. J. Sci.* **1993**, *29*, 61–74.
37. Calder, D.R. Associations between hydroid species assemblages and substrate types in the mangal at Twin Cays, Belize. *Can. J. Zool.* **1991**, *69*, 2067–2074. [[CrossRef](#)]
38. Calder, D.R. Abundance and distribution of hydroids in a mangrove ecosystem at Twin Cays, Belize, Central America. *Hydrobiologia* **1991**, *216*, 221–228. [[CrossRef](#)]
39. Diaz, M.C.; Rützler, K. Sponges: An essential component of Caribbean coral reefs. *Bull. Mar. Sci.* **2001**, *69*, 535–546.

40. Hargitt, C.M. Hydroids of the Philippine Islands. *Philipp. J. Sci.* **1924**, *24*, 467–507. Available online: <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=24462> (accessed on 14 July 2022).
41. Amelia, M.; Suaberon, F.A.; Vad, J.; Fahmi, A.D.M.; Saludes, J.P.; Bhubalan, K. Recent Advances of Marine Sponge—Associated Microorganisms as a Source of Commercially Viable Natural Products. *Mar. Biotechnol.* **2022**, *24*, 492–512. [[CrossRef](#)]
42. Hentschel, U.; Schmid, M.; Wagner, M.; Fieseler, L.; Gernert, C. Isolation and phylogenetic analysis of bacteria with antimicrobial activities from the Mediterranean sponges *Aplysina aerophoba* and *Aplysina cavernicola*. *FEMS Microbiol. Ecol.* **2001**, *35*, 305–312. [[CrossRef](#)]
43. Thoms, C.; Ebel, R.; Proksch, P. Activated chemical defense in *Aplysina* sponges revisited. *J. Chem. Ecol.* **2006**, *32*, 97–123. [[CrossRef](#)]
44. Assmann, M.; Lichte, E.; Pawlik, J.R.; Köck, M. Chemical defenses of the Caribbean sponges *Agelas wiedenmayeri* and *Agelas conifera*. *Mar. Ecol. Prog. Ser.* **2000**, *207*, 255–262. [[CrossRef](#)]
45. Ebel, R.; Brenzinger, M.; Kunze, A.; Gross, H.J.; Proksch, P. Wound activation of protoxins in marine sponge *Aplysina aerophoba*. *Can. Field-Nat.* **1997**, *111*, 1451–1462. [[CrossRef](#)]
46. Weiss, B.; Ebel, R.; Elbrächter, M.; Kirchner, M.; Proksch, P. Defense metabolites from the marine sponge *Verongia aerophoba*. *Biochem. Syst. Ecol.* **1996**, *24*, 1–7. [[CrossRef](#)]
47. Teeypant, R.; Woerdenbang, H.J.; Gross, H.J.; Proksch, P. Biotransformation of the Brominated Compounds in the Marine Sponge *Verongia aerophoba*: Evidence for an Induced Chemical Defense? *Planta Med.* **1993**, *59*, A641–A642. [[CrossRef](#)]
48. Thoms, C.; Wolff, M.; Padmakumar, K.; Ebel, R.; Proksch, P. Chemical Defense of Mediterranean Sponges *Aplysina cavernicola* and *Aplysina aerophoba*. *Z. Fur Naturforsch.* **2004**, *59*, 113–122. [[CrossRef](#)] [[PubMed](#)]
49. Chanas, B.; Pawlik, J.R.; Lindel, T.; Fenical, W. Chemical defense of the Caribbean sponge *Agelas clathrodes* (Schmidt). *J. Exp. Mar. Bio. Ecol.* **1997**, *208*, 185–196. [[CrossRef](#)]
50. Wulff, J.L. Resistance vs recovery: Morphological strategies of coral reef sponges. *Funct. Ecol.* **2006**, *20*, 699–708. [[CrossRef](#)]